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AMERICAN WHITE BUTTERFLIES (PIERIDAE) AND ENGLISH FOOD-PLANTS

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Six years ago (1964), when I offered notes on the rearing of subspecies of *Pieris napi* L., I did so “in spite of their European bias.” What I had in mind was the possible non-availability of recommended food-plants in America, rather than their unsuitability for Nearctic subspecies. However, even before the notes appeared, I had run into trouble with *Pieris virginiensis* Edwards.

Most subspecies of the *Pieris napi* species-group will thrive on a variety of cruciferous plants. Even *bryoniae* Ochseneimer, which in its Alpine habitats feeds almost exclusively on *Biscutella laevigata* L., shows no obvious preference for this plant in captivity, and does quite well on *Alliaria petiolata* Bieb. Other authors (e.g. Hovanitz & Chang 1962) have attempted systematic experiments on the choice of food by *Pieris* larvae (usually *P. rapae* L.), but it is difficult thus to demonstrate the reality of host-species preferences, unless they are sufficiently marked to over-ride possible differences in condition of the plants presented. The experiments and observations now to be described were not systematic in this sense, but by repetition and ruthlessness established certain conclusions.

Pieris virginiensis Edwards

May 1962.—Larvae hatching from Connecticut eggs of *P. virginiensis* (kindly sent by Mr. S. A. Hessel) fed on *Dentaria diphylla* Michx. leaves sent with them, but would do no more than nibble at English *Alliaria*, *Hesperis matronalis* L. and *Cardamine pratensis* L. All died. Later ex-

perience suggests that a maintained supply of *Cardamine* might have saved them.

May 1963.—Paired females from pupae received from S. A. H. laid ca. 200 eggs apparently indifferently on *Dentaria diphylla* and *Alliaria*; these were divided into $v(1)$, $v(2)$ and $v(3)$.

$v(1)$ —Forty-three eggs on *Alliaria* were kept on this plant. Although the larvae began eating the leaves, growth did not continue; many disappeared or died. After ca. 10 days only 2 survived; these were put on *D. diphylla* and then on the very local English *D. bulbifera* L. One nevertheless died; the other recovered and fed up normally (finally on *Cardamine*).

$v(3)$ —One hundred and three eggs on *Alliaria* were further divided. Twenty-four larvae, transferred to *D. diphylla* and thence to *D. bulbifera*, suffered no check. All or most of the larvae remaining on *Alliaria* must have fed slightly, judging by the condition of the leaves; after ca. 5–7 days the three very thin survivors were transferred to *Dentaria*. Two nevertheless died, but one fed up well (finally on *Cardamine*).

$v(2)$ —Eggs on potted *D. diphylla* were transferred to *D. bulbifera* and combined with the first 24 of $v(3)$. Three larvae, just in the last instar, were put on *Hesperis*. After some hours all 3 had left the leaves, which they had not begun to eat. The following day the same 3 larvae were again taken off *Dentaria* and were put on *Alliaria* for 24 hours; a very little of this was eaten, but it was evidently unacceptable. The larvae then fed up normally on *Dentaria*; the last 2 feeding (in Scotland) accepted *Cardamine*.

June 1964.—A further generation was bred from a single paired female. Rearing losses were very high because (1) *Dentaria* had largely died down, (2) the *Cardamine*-producing meadow had been sprayed with weed-killer. Three of the butterflies emerged without diapause.

May 1965.—Broods were obtained from a pair from fresh S. A. H. pupae (v) and by caging 2 such males with 3 females reared in 1964 (u).

u —Eggs were all laid on *Alliaria*, none on *Hesperis* nor on *Dentaria bulbifera*. Some larvae were fed almost entirely on *D. bulbifera*. Others were transferred direct to *Cardamine*: after a slow start these grew well. Still others were transferred first to *Dentaria*, thence to *Nasturtium officinale* R. Br. (watercress), which was accepted.

v —Eggs were all laid on *Alliaria*, none on *Hesperis*. Initial rearing was on *Dentaria*: one larva on *Cardamine* pupated ca. 7 days later than its

contemporaries; two ca. 16 mm long were moved to watercress and of these one at first refused but later accepted it. A few days later the remaining larvae were given watercress. Some larvae ate old *Dentaria* petioles in preference to watercress; here, at least, the species of plant over-rode its condition.

1966-67.—Six more broods were raised, largely on watercress. One in 1967 included a very few eggs laid on *Hesperis* but none on *Cardamine*. One 1966 brood yielded a few "summer" specimens.

P. napi oleracea Harris

May 1964.—A pair, from New Hampshire pupae received from Mr. Hessel, produced only 25 eggs. *Alliaria* was supplied as food, but several larvae died and alternatives were tried: *Sinapis arvensis* L., *Sisymbrium officinale* L. and *Dentaria*. No obvious preference for any of these was shown, but there was no systematic experiment. The 9 butterflies obtained after diapause were all small except one male.

July 1965.—Pairings from 1965 pupae received from S. A. H. produced 3 large broods. The young larvae were failing on *Alliaria*, so were transferred to *Cardamine*, and later to *Sisymbrium* and *Hesperis*. Two small larvae were put on *Alliaria* only; very little was eaten and both larvae were dead in 19 days. One larva which accepted *Alliaria* proved to be an English waif.

P. napi marginalis Scudder

July 1966.—Stocks were raised from pupae (Saddle Mt. State Pk., Oregon) received from Mr. C. W. Nelson. Watercress was used successfully as larval food from the beginning. At first it was thought that *Alliaria* (as well as the horseradish *Armoracia*) had been accepted by the first batch of larvae, but some isolated larvae ate little or none of it. However, even larvae placed on *Sisymbrium* died and it became obvious that part of this brood was unhealthy.

July 1967.—A later brood was given *Cardamine* + *Alliaria*. As the remaining *Cardamine* dried up several small larvae died, but no *Alliaria* was eaten. Thereafter watercress and *Sisymbrium* were substituted.

Another brood all started to feed on *Alliaria*, but only one larva continued to do so, and this ultimately proved to be a Mediterranean stray.

June 1968.—A small batch apparently did well on *Alliaria* while young, but were then given *Sisymbrium* (on which they made slow progress), *Hesperis* and *Nasturtium*. When about 10 days old the larvae were divided: on *Alliaria* all 13 died; on *Nasturtium* 3 died and 13 pupated.

Hybrids

The breeding of hybrids of American subspecies will be described elsewhere; the account is anticipated here only to state that American-British hybrid larvae (both *virginiensis* ♀ × *napi* ♂ and *napi* ♀ × *oleracea* ♂, as well as the reciprocal hybrids of *marginalis* with Irish and British *napi*) fed normally on British food-plants, including *Alliaria*, but *virginiensis* × *oleracea* hybrids rejected *Alliaria*.

Discussion

It has been known for a very long time (Verschaeffelt 1910) that Pierinae feed almost exclusively on plants united in their possession of mustard oils—Cruciferae, Capparidaceae, Resedaceae and Tropaeolaceae. Verschaeffelt also successfully induced larvae to feed on almost pure carbohydrates by flavouring them with juice containing natural mustard oils. Such experiments have often been repeated since, with various degrees of sophistication, and the analyst can now easily distinguish the various mustard-oil glucosides present in different species of Cruciferae, etc.

The evolution of oligophagy has been discussed by Dethier (1954), and the general subject of the co-evolution of butterflies and dicotyledonous plants has been admirably treated by Ehrlich and Raven (1964). As in the quoted case of Papilionids on Aristolochiaceae, it would appear that the Pierinae are a group which developed the ability to cope with a class of toxic or repellent chemical products, which then became, for them, attractants (among mammals, Hominidae appear now to be attracted by many of these same toxins). While the Coliadinae and the Dismorphiinae remained generally attached to Leguminosae, Pierinae diversified in their chosen field and became increasingly selective in respect of the combinations of volatiles demanded in their host-plants. We may suppose that in a relatively stable environment specialization in any one line normally increased until the population became confined to one or two closely related species of plants, though the choice of these might differ between conspecific populations in very different biotas.

If this is so, then we have in *Pieris* examples of "old" and "young" species: *P. virginiensis*, *P. ergane* Geyer and perhaps *P. bryoniae*; *P. rapae* L. and European *P. napi*. *Pieris ergane* provides interesting parallels with *P. virginiensis*. Another fragile butterfly of "relic" distribution, it also has $n = 26$ chromosomes (Lorković 1941—see also 1968) although belonging to the *napi* group which normally has $n = 25$; it also is re-

stricted as to food, in this case to subspecies of *Aethionema saxatile* (L.) R. Br. (Descimon 1966, Lorković 1968). Lorković's females would lay on none of 23 other crucifers.

When an oligophagous American "*napi*" is crossed with a polyphagous European (in either direction), the hybrids are polyphagous. Whether in these cases oligophagy is simply recessive was not determined. The most restricted feeder, *virginiensis*, would have to be used to obtain unequivocal results, but after the F₁ only back-crosses to the supposedly dominant *napi* were obtained.

The association between a butterfly species and its usual host-plant requires that two conditions should be satisfied: (1) the female is attracted to lay her eggs on or near the plant, and (2) the hatched larvae eat it and go on eating it. As we have seen for *P. virginiensis*, females may be super-normally attracted to a plant which the larvae refuse to continue eating. On the other hand the wild females of *P. bryoniae*, by laying their eggs almost exclusively on *Biscutella* (or locally on *Arabis halleri* L.), conceal the readiness of their larvae to accept a wide range of cruciferous plants.

If *Alliaria petiolata* were introduced to the American habitats of *P. virginiensis* it is very probable that females would lay on it initially. Subsequently either a larval variety would appear that tolerated *Alliaria*, or the tendency to lay on *Alliaria* would be eliminated—the latter is much the more likely sequel. In either case the cost of re-adaptation might be very heavy.

It is clear that the inappropriate laying of captive females on *Alliaria* is connected with the absence of this plant from the *virginiensis* habitat—otherwise the indiscriminating behaviour could not have persisted. Straatman (1962) has reported instances of four species of Australian Lepidoptera laying in the wild on introduced plants; the general sequence was that the larvae nibbled, refused to continue feeding and ultimately died. In spite of the title of his notes, Straatman provides no evidence that the plants were toxic to the larvae; it is more likely that his cases were entirely analogous to our experiments with *virginiensis*.

The other "whites," *oleracea* and *marginalis*, are not as restricted in their choice of Cruciferae, though neither will continue to feed adequately on *Alliaria*. *P. n. oleracea* has a wider range of known host-plants than *virginiensis*, and does include the latter's *Dentaria diphylla*. The survival of *virginiensis* where the two species are sympatric depends upon its closer adaptation to life in the shady woods where *Dentaria* grows (Rothke 1931, Voss & Wagner 1956). In England *P. napi* does lay on

Dentaria bulbifera, but rarely, the habitat being rather too densely wooded.

In the wild, *P. virginiensis* is reputed to be almost invariably univoltine, though as we have seen it is potentially bivoltine. Since *Dentaria diphylla* is a "spring" plant, dying back early in June, butterflies which inherited a tendency to emerge in summer would have little chance of reproduction if the larvae are in practice confined to *Dentaria*. A selective process will account for the failure of this rather southern species to produce two generations in the year, which it could otherwise easily do.

It would be of some interest to establish a colony of *P. virginiensis* in Europe. If the attempt is made it should be in an area where *Dentaria* is commoner than in England. It is to be expected that initially rather free pairing with the local *P. napi* would occur, giving polyphagous hybrids. If *Alliaria* were present, part of the eggs would be deposited on it, and of these only the hybrids and back-crosses to *napi* would survive. The colony might be wiped out before a barrier of sexual discrimination could be built up. The experiment would be permissible, with such an unaggressive insect as *virginiensis*.

Summary

Not all British Cruciferae on which European *P. napi* and *bryoniae* subspecies can be raised are accepted by larvae of the American *P. napi oleracea*, *P. n. marginalis* and *P. virginiensis*. *Alliaria petiolata*, on which *P. virginiensis* actually lays preferentially, is initially attractive but larvae will not continue to eat enough of it and die of inanition. However, *Cardamine pratensis* and *Nasturtium officinale* are eaten, and the latter is recommended. In addition, *Hesperis* and *Sisymbrium* can be used for *oleracea* and *marginalis*.

European-American hybrids feed normally on *Alliaria*.

P. virginiensis is univoltine in the wild in consequence of its restriction to a "spring" plant, *Dentaria*.

The choice of food-plants by Pierinae is discussed. In a relatively stable environment, a species tends to become adapted to a very limited range of hosts. For the larvae, though perhaps not for the laying female, the optimum concentration of the attractants may be exceeded in certain plants, so that feeding ceases; or alternatively a still intolerable repellent compound may accompany the attractants.

The very specialised *P. virginiensis* has probably become increasingly adapted, over hundreds of thousands of years, to an unchanging habitat;

now its archaic condition threatens its survival. On the other hand *Pieris napi* has kept its evolutionary mobility and its subspecies have occupied a variety of environments, some still changing rapidly; in that sense the species has retained its youth.

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THE BRAZILIAN "CERCYONIS" (SATYRIDAE)

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Much confusion has occurred in the delimitation of the genus *Cercyonis* Scudder (1875). Periodically various authors have sought to unite these American butterflies with the Palearctic *Satyrus* Latreille (1810), and *Minois* Hübner (1819) whereas other authors have pointed out the distinctness of *Cercyonis*. Miller (1968, pp. 99, 120) showed that the Nearctic *Cercyonis* are members of the satyrine tribe Maniolini, and in fact, the only American representatives of this basically Palearctic tribe,